Figures 30–33. Holotype shells of species of *Owengriffithsius* Emberton gen. nov., all to same scale. Figure 30. *Owengriffithsius tsaratananae* Emberton, sp. nov., in three views (UF 285426). Figure 31. *Owengriffithsius griffithsi* Emberton, sp. nov., in four views (UF 285430). Figure 32. *Owengriffithsius namorokae* Emberton, sp. nov. (UF 285424). Figure 33. *Owengriffithsius orchidae* Emberton, sp. nov. (UF 285428). Scale bar 1 mm.

Type locality: Madagascar, Tsaratanana Reserve, 14°02′S, 48°47′E, 1100 m, rainforest, 15 June 1995.

Description of holotype shell (Figure 30; aperture broken; measurements taken at latest complete aperture): Juvenile. Diameter 5.4 mm, height 5.9 mm, whorls 4.9, umbilicus 0.6 mm. Spire high concave-conic, apex slightly mamillate. Body-whorl periphery round; suture deeply impressed, a V-shaped channel, beginning at shell's very apex; whorl shoulders rounded. Aperture apparently round; height 3.0 mm, width 2.9 mm. Apertural lip unreflected, except slightly at columella. Embryonic whorls 2.5; first 1.5 whorls 1.13 mm in diameter. Embryonic sculpture: initial 0.5 whorl smooth, then weak dense riblets dissected by dense, engraved spiral lines. Body-whorl sculpture smoothish, with minute, parallel, fairly evenly and densely spaced spiral cordlets separated by narrow

grooves, wavy and/or slightly interrupted where they cross the faint, densely but unevenly spaced, unevenly weak axial growth striae. General color light yellowish brown; apex slightly darker and more reddish.

Shell variation: See Table 1.

Etymology: For Tsaratanana Reserve.

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Geographic Variation of Shell Geometry in the Abyssal Snail
Xyloskenea naticiformis (Jeffreys, 1883)

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Abstract. Very little is known about population differentiation in abyssal species. We measured Raup's parameters of shell geometry to document geographic variation in lower bathyal and abyssal populations of the archaeogastropod *Xyloskenea naticiformis* collected in the western North Atlantic. We performed an ANOVA with multiple comparisons to test for interpopulation differences in four basic descriptors of shell form: shape of the generating curve, rate of whorl expansion, position of the generating curve in relation to the coiling axis, and rate of translation. A quantified Jaccard's Coefficient was used to combine the four parameters into a metric of interpopulation phenotypic similarity that was regressed against depth difference and horizontal distance among samples to examine the effects of geographic separation. Overall, geographic variation is muted compared to bathyal deep-sea and coastal marine snails. Significant variation in shell form is largely attributable to a depth difference of 800–1000 m between the lower bathyal zone and the abyssal plain. Abyssal populations show only subtle variation on large (100s km) spatial scales. Results support the theory that population differentiation in mollusks decreases with increasing depth in the deep sea, and that the abyss is less conducive than the bathyal zone to evolutionary divergence in the western North Atlantic.

INTRODUCTION

It is now well established that the deep sea supports a highly diverse and endemic benthic invertebrate fauna (Hessler & Sanders, 1967; Etter & Mullineaux, 2001), and that community structure varies on local (Grassle & Maciolek, 1992), regional (Etter & Grassle, 1992), and global (Rex et al., 2000) scales. Only recently has attention been devoted to the general problem of how this rich and remarkable fauna evolved (Etter & Rex, 1990; France, 1993; Chase et al., 1998). The primary evidence for understanding patterns of speciation in terrestrial and shallow-water biotas is geographic variation within individual species (Mayr, 1966; Gould & Johnston, 1972; Slatkin, 1987; Palumbi et al., 1997). Documenting and interpreting geographic variation in deep-sea species have proven difficult, particularly at abyssal depths (> 4000 m) where most are very sparsely distributed, and sampling has been limited. In this paper, we analyze geographic variation in shell form of a common and broadly distributed abyssal snail *Xyloskenea naticiformis* (Jeffreys, 1883), collected from the North American Basin of the Atlantic Ocean. Patterns of geographic variation in *X. naticiformis* provide information of basic interest on population differentiation in abyssal species.

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MATERIALS AND METHODS

Xyloskenea naticiformis is a minute trochiform archaeogastropod belonging to the family Skeneidae (Warén, 1996). It is widespread at abyssal and bathyal depths of the Atlantic (Warén 1996) and is the second most abundant gastropod species at abyssal depths in the North Atlantic Basin (Rex & Warén, 1982). As with most deep-sea species, little is known of its natural history. The larval shell consists of a single simple whorl measuring 250 µm in maximum diameter (Figure 1). This indicates a non-planktotrophic mode of development (Bouchet & Warén, 1994). Whether or not there is a non-feeding pelagic dispersal stage cannot be determined from larval shell morphology in archaeogastropods (Hadfield & Strathmann, 1990). The broad distributions of many deep-sea archaeogastropods and their frequent association with ephemeral patchy habitats (McLean, 1992; Warén & Bouchet, 1993; Warén, 1996; Marshall, 1994) would seem to require dispersal, which in cold bottom currents could involve considerable distances (Hoegh-Guldberg et al., 1991; Shilling & Manahan 1991; Welborn & Manahan, 1991). In every case where a substrate is known, members of the genus *Xyloskenea* in the deep sea are associated with sunken wood (Warén, 1996). There is no record of wood occurring in the samples analyzed here, but this could easily represent a sampling bias. The relatively high abundance and consistent occurrence of *X. naticiformis* in abyssal samples from the western North Atlantic suggest that it might be a facultative deposit feeder as well as grazing on plant debris.

Figure 1. Apical view of a specimen of *Xyloskenea naticiformis* from station 124 (see Table 1 for station data). The arrow indicates the terminus of the larval shell. The larval shell measures 250 μm in maximum width, and the adult shell 1.66 mm in maximum width.

We measured shell form of 152 specimens of *Xyloskenea naticiformis* collected with an epibenthic sled (Hessler & Sanders, 1967) from eight sampling stations in the western North Atlantic (Table 1, Figure 2). One station (85) is located at 3834 m on the lower continental rise, and the other seven are abyssal (4680–4862 m). Our selection criterion was simply to measure all available specimens in sufficiently good condition for samples with ≥ nine such individuals (*X. naticiformis* appeared in seven other samples in this depth range, but with only one to two individuals per sample, which does not permit statistical comparison). The distribution of samples allows us to examine geographic variation in shell form over horizontal scales of up to 100s of kilometers (4–483 km) and bathymetric scales up to about 1000 m (1–1028 m).

In our earlier analyses of geographic variation in deepsea snails, e.g., Rex et al., 1988; Rex & Etter, 1990 we quantified shell form using an approach developed by Gould (1969) in which shell size, shape, and sculpture are standardized to common growth stages. These standardized measurements were referenced to the terminus of the protoconch which marks the transition from larval to adult growth. These analyses were conducted on rissoids and turrids which have relatively high-spired shells so that much of each whorl is exposed for taking measurements. The shells of *Xyloskenea naticiformis* require a different approach. They lack conspicuous sculpture and are much more globular so that early whorls are more obscured by subsequent growth (Figures 1 and 3). Also, in larger specimens, corrosion often makes the adult-larval transition difficult or impossible to discern so that accurate measurements cannot be taken at common growth stages on the adult shell.

However, the simple unadorned shells of *Xyloskenea naticiformis* can be used to estimate Raup's (1966) basic parameters of shell geometry. To measure these parameters we made camera lucida drawings of the shells (at ×50) in two orientations (Figure 3). Following Raup (1966) and Newkirk & Doyle (1975), we approximated the four basic parameters of shell form using the measurements indicated in Figure 3:

(S) Shape of the Generating Curve. This is expressed as a ratio of the width of the aperture to the height of the aperture.

(W) Rate of Whorl Expansion. Raup (1966) defined this as:

$$W = \left(\frac{r_2}{r_1}\right)^{2\pi/\theta}$$

where r_1 and r_2 are radii from the axis of coiling to corresponding points on the generating curve (in this case the outer margin of whorls) separated by an angular distance of θ radians. We measured radii (OS and OE in Figure 3) every 45°, so the appropriate exponent ($2\pi/\theta$) is eight. Estimates of W were averaged for each individual (mean = 14, range 8–17 values).

(D) Position of the Generating Curve in Relation to the Coiling Axis. In most prosobranchs the whorls are wound tightly with the inner margins in contact so that D is zero. In umbilicate snails like *Xyloskenea naticiformis,* D is the rate at which whorls move away from the axis of coiling, creating a cone-shaped opening that extends from the bottom of the shell toward the apex. D is the ratio of the radius at the inner margin of the whorl to that at the outer margin. Again these ratios were measured every 45° and averaged (mean = 15, range 9–18 values).

(T) Rate of Translation. This is the rate at which whorls move down the axis of coiling in helicoid shells. Raup (1966) defined it as dy/dr, where dy is the distance which the center of the generating curve moves down the coiling axis, and dr is the distance which it moves away from the axis. Since it is difficult to locate the center of the generating curve of successive whorls, we followed Newkirk & Doyle (1975) in approximating T as the ratio of height of the axis of coiling to the radius (Figure 3).

Averages and standard deviations for S, W, D, and T in all eight populations are given in Table 1.

We performed an ANOVA and Sheffé multiple comparisons among stations for all four variables to test the null hypothesis of no difference in shell form among populations. To get a more general composite picture of interpopulation differentiation, we combined all four parameters of shell geometry into a single measure of phenotypic similarity by using a quantified Jaccard's Coefficient (Sepkoski, 1974) calculated on the average values
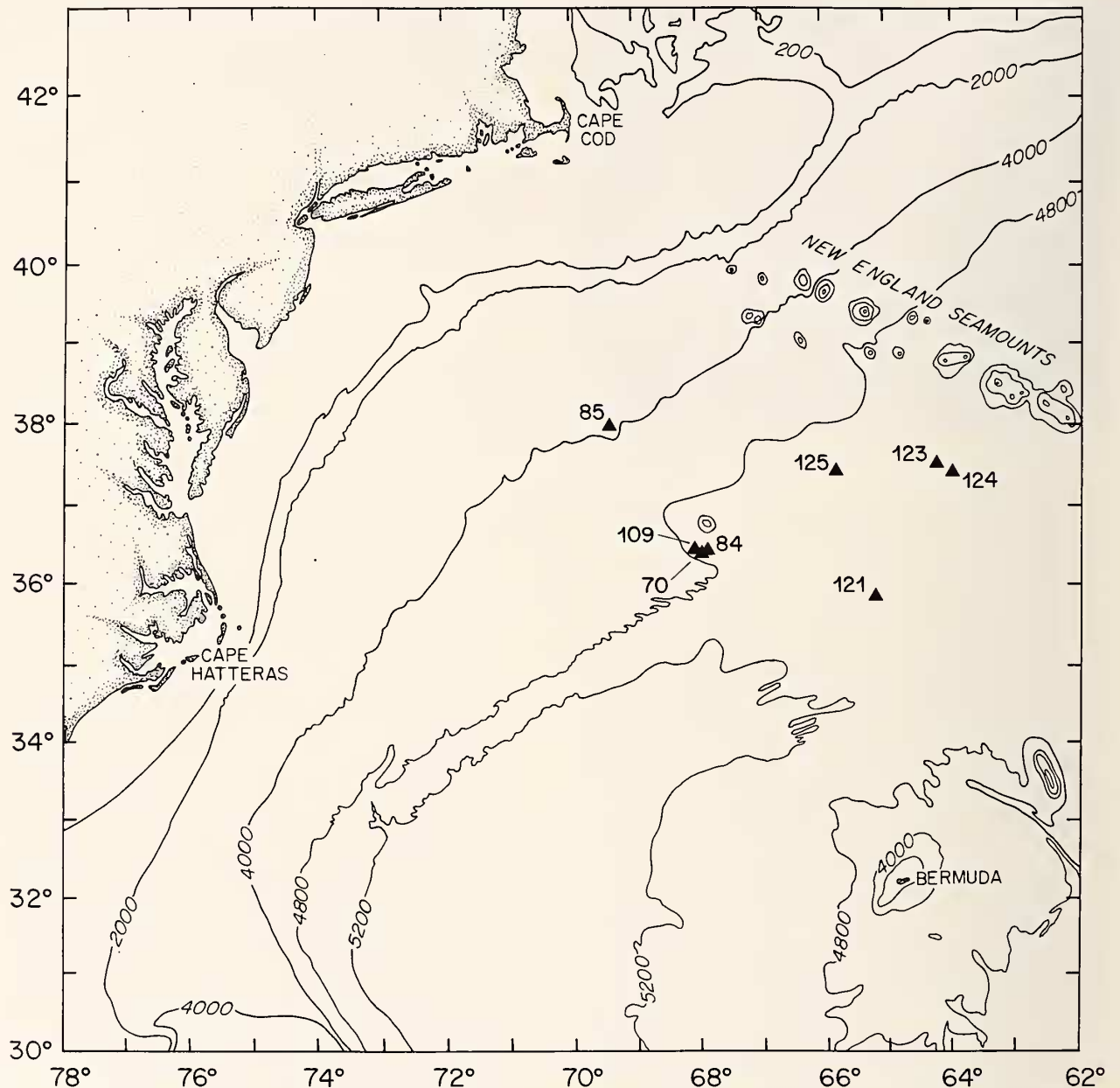
Figure 2. Map of deep-sea benthic stations where samples of *Xyloskenea naticiformis* analyzed in this study were collected. See Table 1 for station data.

shown in Table 1. To assess whether the degree of phenotypic difference among populations corresponds to the degree of geographic separation, we carried out a multiple regression with Jaccard's Coefficient as the response variable, and depth difference and horizontal distance apart as explanatory variables.

RESULTS AND DISCUSSION

Mean values for the four variables of shell form are presented in Table 1. Shells from all localities have very similar generating curves (width to height ratios of apertures are close to one, Table 1). However, shells from station 85 (at 3834 m) stand out as being uniquely different from all abyssal populations in having a more globular shape: translation rates are lower and whorl expansion rates are higher. Values of D are also lower in station 85, i.e., the umbilicus is relatively less well developed because of the higher rate of whorl expansion. The ANOVA reveals a weak overall difference in S, and highly significant differences among samples for the other three
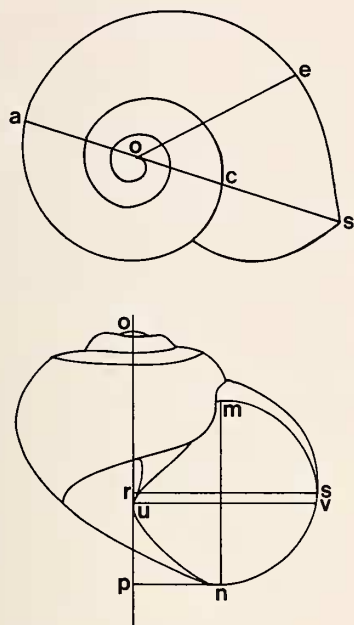
$$S = (\overline{uv}/\overline{mn}) \quad W = (\overline{os}/\overline{oe})^8 \quad D = (\overline{oc}/\overline{os}) \quad T = (\overline{or}/\overline{os})$$
$$\text{height} = \overline{op} \quad \text{width} = \overline{aos} \quad \angle eos = 45°$$

Figure 3. Apical and apertural views of *Xyloskenea naticiformis* showing the measurements taken to estimate Raup's (1966) four basic parameters of shell geometry. See text for an explanation of the variables and how shells were measured.

variables (Table 2). Multiple comparison tests show that these differences are largely attributable to station 85 which differs from selected abyssal stations in the same directions noted above (Table 2).

Phenotypic similarity measured as the quantified Jaccard's Coefficient is significantly and negatively correlated with depth differences among samples ($r = -0.44$, $F_{1,26} = 6.283$, $P = 0.019$) due to the distinctiveness of the population from station 85 and the large depth sepa-

Table 2

ANOVA with multiple comparisons for Raup's (1966) four basic parameters of shell geometry (S, W, D, T) for populations of *Xyloskenea naticiformis* in the western North Atlantic. See Table 1 for station data. The inequality signs for the multiple comparison tests indicate a significant ($P < 0.05$) difference and the direction of the difference.

Variable	df	F	Significance	Multiple comparison
S	7,144	2.210	$P = 0.0367$	
W	7,144	3.524	$P = 0.0016$	85 > 121
D	7,144	3.892	$P = 0.0006$	85 < 84
T	7,144	3.489	$P = 0.0017$	85 < 123

ration ($\sim$800–1000 m) between station 85 and abyssal stations. The degree of phenotypic similarity is unrelated to horizontal separation ($F_{1,26} = 3.785$, $P = 0.063$). A multiple regression with both distance and depth included as explanatory variables is marginally significant ($F_{(2,25)} = 3.56$, $P = 0.044$).

When the ANOVA is performed on only abyssal stations, differentiation among samples is still detectable, but at a lower level of statistical significance. Translation rate no longer varies significantly ($F_{6,125} = 1.925$, $P = 0.082$). The parameters S, W, and D show significant variation among samples ($P = 0.028$, 0.008, and 0.017, respectively) with multiple comparison tests detecting a difference in only one case (for W, 121 < 124). For abyssal samples, the degree of phenotypic similarity is not related significantly to either depth difference ($F_{1,19} = 0.424$, n.s.), or distance apart ($F_{1,19} = 0.433$, n.s.). A multiple regression analysis using both depth difference and distance is not significant ($F_{2,18} = 1.518$, n.s.).

In summary, the clearest divergence in shell form is associated with the large bathymetric difference (800–1000 m) between station 85 on the continental rise and

Table 1

Station data, sample size (n), and the means ($\bar{x}$) and standard deviations (SD) of Raup's (1966) four basic parameters of shell geometry (S, W, D, T) for populations of *Xyloskenea naticiformis* examined in this study. See Figure 2 for a map of station localities. See the text and Figure 3 for a description of the variables and their measurement.

Station	Depth (m)	Latitude (N)	Longitude (W)	n	S $\bar{x}$	(SD)	W $\bar{x}$	(SD)	D $\bar{x}$	(SD)	T $\bar{x}$	(SD)
85	3834	37°59.2′	69°26.2′	20	0.985	(0.048)	2.285	(0.221)	0.416	(0.032)	0.794	(0.085)
70	4680	36°23.1′	67°58.0′	14	0.976	(0.076)	2.210	(0.107)	0.434	(0.013)	0.833	(0.062)
84	4749	36°24.4′	67°56.0′	30	0.971	(0.059)	2.160	(0.138)	0.442	(0.016)	0.869	(0.078)
109	4750	36°25.0′	68°06.0′	9	1.001	(0.089)	2.158	(0.053)	0.424	(0.017)	0.876	(0.074)
121	4800	35°50.0′	65°11.0′	12	0.963	(0.071)	2.053	(0.102)	0.438	(0.015)	0.838	(0.130)
125	4825	37°25.0′	65°52.0′	35	0.978	(0.044)	2.190	(0.160)	0.430	(0.018)	0.861	(0.063)
123	4853	37°29.0′	64°14.0′	15	1.025	(0.056)	2.173	(0.106)	0.429	(0.011)	0.912	(0.066)
124	4862	37°25.0′	63°58.0′	17	1.014	(0.062)	2.244	(0.095)	0.439	(0.017)	0.839	(0.073)